



# Feedbacks between soil penetration resistance, root architecture and water uptake limit water accessibility and crop growth – A vicious circle

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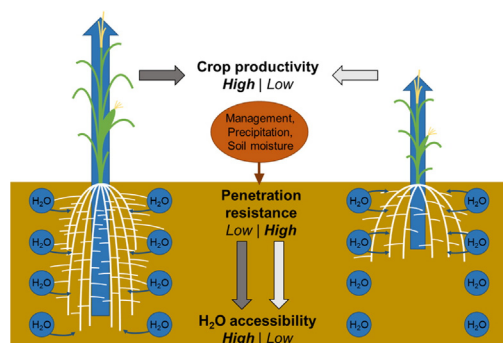
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## HIGHLIGHTS

- Maize root systems became shallower due to increased topsoil penetration resistance.
- Shallower root systems led to increased water uptake from the topsoil.
- In turn, penetration resistance further increased, which impeded deeper root growth.
- This feedback eventually reduced water accessibility and crop productivity.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Water is the most limiting resource for global crop production. The projected increase of dry spells due to climate change will further increase the problem of water limited crop yields. Besides low water abundance and availability, water limitations also occur due to restricted water accessibility. Soil penetration resistance, which is largely influenced by soil moisture, is the major soil property regulating root elongation and water accessibility. Until now the interactions between soil penetration resistance, root system properties, water uptake and crop productivity are rarely investigated. In the current study we quantified how interactive effects between soil penetration resistance, root architecture and water uptake affect water accessibility and crop productivity in the field. Maize was grown on compacted and uncompacted soil that was either tilled or remained untilled after compaction, which resulted in four treatments with different topsoil penetration resistance. Higher topsoil penetration resistance caused root systems to be shallower. This resulted in increased water uptake from the topsoil and hence topsoil drying, which further increased the penetration resistance in the uppermost soil layer. As a consequence of this feedback, root growth into deeper soil layers, where water would have been available, was reduced and plant growth decreased. Our results demonstrate that soil penetration resistance, root architecture and water uptake are closely interrelated and thereby determine the potential of plants to access soil water pools. Hence, these interactions and their feedbacks on water accessibility and crop productivity have to be accounted for when developing strategies to alleviate water limitations in cropping systems.

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Water scarcity is the most important constrain to global crop production and food security. The predicted increase of droughts in the course of climate change will further aggravate the problem of water-limited crop yields (Bates et al., 2008). Water is taken up from soil via the plant's root system, from where water is then distributed to all other plant organs. Plants may suffer from water shortage due to different soil-borne reasons, namely low water abundance, low water availability and restricted accessibility to soil water. Hence, different phenomena may induce water-limited crop yields. Water abundance describes the amount of water in the soil. Water availability refers to the proportion of soil water that is available to plants, hence to the water that may potentially be extracted by plant roots. Water accessibility refers to the ability of plant roots to reach plant available water, and is determined by different processes and interactions in the soil–plant system (Bengough et al., 2011). Water abundance and availability can be quantified directly under field conditions using in-situ instrumentation, and their effects on plant growth and agricultural productivity are studied extensively. In contrast, water accessibility cannot be quantified directly, and the effects of restricted water accessibility on plant growth and agricultural productivity received only little attention so far.

Soil penetration resistance is the main soil property that determines water accessibility since it largely regulates root elongation rates. It therefore determines whether, how fast and at which metabolic costs roots may reach soil water pools (Atwell, 1990; Bengough et al., 2011; Grzesiak et al., 2014; Colombi et al., 2017b). Soil penetration resistance is positively correlated to soil bulk density. Hence, elevated soil penetration resistance is characteristic for plough pans resulting from long-term tillage, dense topsoil in no-till systems, and compacted soil caused by intensive field traffic (Karunatilake et al., 2000; Hernandez-Ramirez et al., 2014; Martínez et al., 2016; Keller et al., 2017). Furthermore, high soil penetration resistance may also occur in subsoil layers, which are usually denser than the topsoil (White and Kirkegaard, 2010; Lynch and Wojciechowski, 2015). Soil penetration resistance is also strongly influenced by soil moisture as soil penetration increases upon soil drying (Bengough et al., 2011; Grzesiak et al., 2013). Therefore, soil penetration resistance fluctuates during a cropping season due to precipitation events and evapotranspiration. Ultimately root elongation rates decrease in response to increased soil penetration resistance leading to restricted access to soil resources such as water and nutrients (Araki and Iijima, 2005; Bengough et al., 2011; Lipiec et al., 2012; Valentine et al., 2012; Nosalewicz and Lipiec, 2014; Siczek et al., 2015; Colombi et al., 2017b). For monocotyledonous crops such as maize, wheat or rice, penetration resistance in the topsoil is of particular relevance due to their root system architecture that is dominated by adventitious roots. These roots, which are referred to as nodal roots, are initiated in the stem close to the soil surface (Kutschera and Lichtenegger, 1960; Abendroth et al., 2011). Hence, these roots are exposed to topsoil conditions upon initiation. In order to reach lower soil layers to acquire water from deeper soil strata, each newly initiated root needs to penetrate the entire soil profile.

Previous studies have shown that root elongation rates are significantly decreased even if soil penetration resistance is just moderately increased (Bengough et al., 2011; Lipiec et al., 2012; Valentine et al., 2012; Colombi et al., 2017b). With increasing soil penetration resistance, roots need to exert higher forces and mechanical stresses to penetrate soil, leading to increased metabolic costs of soil exploration (Atwell, 1990; Bengough et al., 2011; Ruiz et al., 2016, 2015; Colombi et al., 2017b). Further impacts of increased soil penetration resistance on the root phenotype of a wide range of crops are shallower root growth, thickening of roots and a reduction of both lateral and axial root number (Materrechera et al., 1992; Tracy et al., 2012; Chen et al., 2014; Hernandez-Ramirez et al., 2014; Nosalewicz and Lipiec, 2014; Pfeifer et al., 2014; Colombi and Walter, 2016, 2017). Decreased root elongation rates, shallower root growth, root thickening and decreased root numbers reduce the soil volume that can be explored by plants.

Plant growth and crop performance may significantly decrease as a result of this limited potential to exploit soil derived resources. Decreased plant growth and yields in response to increased soil penetration resistance were observed under both laboratory and field conditions in different major crop species including maize, wheat and soybean (Barraclough and Weir, 1988; Young et al., 1997; Botta et al., 2010; Grzesiak et al., 2013; Colombi and Walter, 2016, 2017; Colombi et al., 2017a).

While impacts of soil penetration resistance on root properties and crop performance have been investigated in numerous studies, the interactions between root architecture, plant water uptake, soil moisture and penetration resistance are rarely looked at. Especially under field conditions, conclusive information about the impact of these interactions on water accessibility and crop performance are missing. Such knowledge is needed to better understand effects of different tillage systems, soil compaction due to field traffic and future climate scenarios on soil resource accessibility and crop productivity. Based on this premise, mitigation strategies may be developed that can alleviate the adverse impacts of decreased water resources on crop production. Detailed plant phenotyping, which encompasses the simultaneous assessment of multiple traits of a plant, in combination with quantification of environmental properties is a well suited approach to better understand plant–environment interactions (Rahaman et al., 2015; Walter et al., 2015; York and Lynch, 2015). Under field conditions, quantifications of root system architecture, which describes the spatial configuration of coarse structures in the soil (Lynch, 1995), can be combined with investigations on plant vigour and water and nutrient uptake. Such approaches enabled to show how different root phenotypic traits are related to plant productivity in response to low nutrient and water availability (Miguel et al., 2013; Saengwilai et al., 2014; Gao and Lynch, 2016). In addition to manual quantifications, automated image processing may be used to extract more complex information about the structure and spatial configuration of entire root systems or single roots at high throughputs (Zhong et al., 2009; Grift et al., 2011; Bucksch et al., 2014; Colombi et al., 2015). These studies clearly demonstrated that combining plant phenotyping with quantifications of soil properties is a suitable approach to improve our understanding on how belowground processes affect plant growth and crop productivity.

In the current study, maize was grown in the field under four different soil physical conditions. These different soil conditions were achieved by applying two tillage systems – mouldboard ploughing and no-till – to compacted and uncompacted soil, resulting in four experimental treatments. We aimed to i) quantify the interactions and feedbacks between soil penetration resistance, root architecture and plant water uptake, and ii) evaluate how these interactive effects affect water accessibility and crop performance. Root system architecture and rooting depth was quantified at flowering using both manual measurements and image processing. Soil moisture was recorded in-situ throughout the cropping season and soil penetration resistance was determined on undisturbed soil cores at different soil matric suctions. This allowed periods of the cropping season during which soil penetration resistance exceeded certain thresholds to be determined. Quantifications of aboveground plant growth, plant vigour at flowering and silage yield complemented the measurements.

## 2. Material and methods

### 2.1. Site description, experimental design and growth conditions

The study was carried out in the Soil Structure Observatory (SSO; Keller et al., 2017), located at Agroscope Zurich, Switzerland (8°31'E, 47°27'N, 443 m above sea level). The soil is classified as a pseudogley Cambisol with a loamy texture (approximately 25% clay, 50% silt and 25% clay) and an organic carbon concentration of 1.7% and a pH (CaCl<sub>2</sub>) of 6.9 in the topsoil. The SSO was established in spring 2014 as a long-term field experiment with three blocks (n = 3) to study the

evolution of soil structure after a compaction event. Compaction was carried out using a heavy four-wheeled agricultural vehicle with a wheel load of 80 kN in March 2014. After compaction, different soil management treatments, including a crop rotation with conventional tillage to 0.22 m depth and no tillage, respectively, were established. This resulted in four different experimental treatments: compaction without tillage (C-NT), compaction with tillage (C-T), no compaction without tillage (NC-NT) and no compaction with tillage (NC-T). The plots are 12 m wide and 17 m long (for more information see Keller et al. (2017)). Summer triticale ( $\times$  *Triticosecale*) was grown in the SSO in the first year after compaction in 2014 (Colombi and Walter, 2016), which was not part of the current study.

A commercial maize hybrid (*Zea mays* L., variety LG30.222) was sown on 25 May 2015. Peak flowering, representing the transition from vegetative to generative plant development, was reached 64 days after sowing (DAS) on 28 July. Fertilisation, sowing density and crop protection measures were done according to local on-farm practice (Table 1). On 28 September, which corresponded to 126 DAS, the crop was harvested as silage maize. From sowing to harvest, mean day and night temperatures were 24.2 °C and 13.3 °C, respectively, and precipitation was 262 mm.

## 2.2. In-situ soil moisture measurements

Soil matric suction was continuously recorded using calibrated heat dissipation sensors (pF-Meter, ecoTech GmbH, Bonn, Germany) in one experimental block, starting three weeks after sowing until harvest. Two probes per depth were installed in each plot at 10, 20 and 40 cm depth. Data were recorded in 30-min intervals using data loggers (Campbell Scientific Ltd., Logan, UT, USA). Daily mean values of soil matric suction were calculated for each depth and treatment, which were then used for further analyses.

## 2.3. Soil penetration resistance, bulk density and porosity

To relate soil matric suction to soil penetration resistance, cone penetrometer tests were performed on undisturbed soil cores that were sampled in the field and equilibrated to different soil matric suctions. After the plants had established, undisturbed soil cores of 5.1 cm diameter and a volume of 100 cm<sup>3</sup> were sampled at 10 cm depth from the four treatments in all three blocks. In the laboratory, the undisturbed soil samples were slowly saturated from below and equilibrated to matric suctions of 300 hPa on a ceramic suction plate, and to 1000, 2000 and 5000 hPa on ceramic pressure plates. For all suctions tested, two samples per plot were prepared. At each level of matric suction, three individual cone penetrometer insertions per sample were carried out. Cone penetration measurements were carried out in the apparatus described by Ruiz et al. (2016). The cone was connected to a force transducer (LC703, OMEGA Engineering Inc., Stamford, CT, USA) and had a recessed shaft, a semi-apex angle of 15° and a cone base radius of 1 mm. The cone was inserted into the soil at a speed of 4 mm min<sup>-1</sup> until a penetration depth of approximately 2 cm was reached.

Penetration force was recorded from the point at which the cone was fully inserted into the soil, resulting in approximately 600 force measurements per cone insertion. The average penetration force for each sample and matric suction was calculated, and converted to soil penetration resistance by dividing the average force by the cone base area.

Linear regressions between matric suction and soil penetration resistance enabled to determine matric suctions at which penetration resistance exceeded a certain threshold. According to previous studies summarised by Bengough et al. (2011) an increase in soil penetration resistance from 1 MPa to 2 MPa and 3 MPa causes root elongation rate to decrease by around 50% and 70%, respectively. Therefore, we used these two values as critical thresholds in the current study. Using this information and the in-situ soil moisture recordings, allowed periods during which soil penetration resistance exceeded 2 MPa and 3 MPa, respectively, to be determined.

Soil dry bulk density was determined on the soil cores that were used for cone penetration tests. After the cone penetration tests, the samples were oven-dried at 105 °C for at least three days and weighed. Additional soil cores were sampled at 30 cm depth, and used to obtain bulk density. Particle density was measured in each block and depth, and used to calculate total porosity for all four treatments at 10 and 30 cm depth. To compare soil water storage across the four treatments, volumetric soil water content was determined at saturation and matric suctions of 30, 100, 300, 1000, 2000, 5000 and 15,000 hPa. The amount of plant available water was then obtained as the difference in volumetric water content between 100 hPa (field capacity) and 15,000 hPa (permanent wilting point) (e.g. Reynolds et al., 2009).

## 2.4. Maize phenotyping

Plant growth was determined in five adjacent plants per plot in two-day intervals starting on 12 June, which corresponded to 18 DAS and the 2-leaf stage, until flowering on 28 July (64 DAS). Plant height measurements from fixed reference points at the soil surface to the collar of the youngest leaf, and leaf numbers were used to quantify plant growth. Four representative non-adjacent plants in each plot were selected for final plant height measurements on 10 August, which corresponded to 77 DAS. Leaf greenness was determined by SPAD measurements as an indicator for leaf nitrogen content (SPAD-502, Konica Minolta, Tokyo, Japan). Three measurements were performed along the blade of the leaf above the husk, and averaged. Stem diameter measured with a sliding calliper was taken as an additional plant vigour parameter before the stalk was cut 20 cm above the soil surface.

The root crowns of these four plants were split in half perpendicular to the crop rows and excavated in a cylinder of approximately 30 cm diameter and depth as described in Colombi et al. (2015). The root crowns were soaked in soap water for 30 min and then cleaned from soil to quantify root system architectural properties. Manual phenotyping included the number of whorls occupied with nodal roots and the number of nodal roots that penetrated the soil. The number of first order lateral roots was assessed in one nodal root from the third whorl of each root crown as a measurement for the branching density of the root system.

**Table 1**

Overview of post compaction treatments, agronomy and basic maize phenology in 2015 in the Soil Structure Observatory (SSO) at Agroscope Zürich, Switzerland.

	Treatments			
	C-NT	C-T	NC-NT	NC-T
Compaction	Yes, March 2014	Yes, March 2104	No	No
Tillage	No	Yes, 22 cm depth, April 2014 and May 2015	No	Yes, 22 cm depth, April 2014 and May 2015
Mineral fertilisation	N: 113.4 kg ha <sup>-1</sup> , P: 20.1 kg ha <sup>-1</sup> , K: 124.5 kg ha <sup>-1</sup> , Mg: 4.6 kg ha <sup>-1</sup>			
Planting density	90'000 plants ha <sup>-1</sup>			
Sowing	25 May			
2-leaf stage	12 June (18 DAS)			
Peak flowering, 50% of individuals	28 July (64 DAS)			
Harvest, silage	28 September (126 DAS)			

Abbreviation: DAS = days after sowing.



To do so, lateral roots were counted in segments of 2 cm length starting at 4 cm and 9 cm, respectively, from the root base. The opening angle of the root crown was determined as a global measurement of nodal root growth directions. The opening angle was determined along a circle of 10 cm radius with the angle vertex set at the centre of the stalk at the soil surface. In addition to these manual measurements of root system architecture, further architectural parameters were determined from RGB pictures using the software *REST* (Colombi et al., 2015). Half-cut root crowns and nodal roots from the third whorl, which were used for the measurement of branching density, were imaged on a blue background. Pictures were captured with an 18-megapixel camera (Canon EOS 600D; Canon, Tokyo, Japan; lens: EF-S18-55mmf/3.5–5.6 ISII; Canon, Tokyo, Japan) fixed to a focal length of 35 mm at a resolution of 90  $\mu\text{m}$  pixel edge length under constant illumination. The maximum width of the root crown, a parameter provided by *REST*, was taken as a measure for the lateral spread of the root crown. Two image-derived parameters were used from pictures of single nodal roots from the third whorl. First, the median size of enclosed background gaps within the root was taken as a global value for branching density of the roots. Second, cluster diameter distributions obtained from the distance map of the root provided information on overall root thickness. In the current study, we used the 1<sup>st</sup> quartile of cluster diameters as a measure for overall root diameter.

One week after root crown sampling (84 DAS), soil cores of 5 cm diameter were taken with a petrol run driller (humax Bohrsonden, Martin Burch AG, Rothenburg, Switzerland) from the soil surface to 62.5 cm depth to measure rooting depth and root biomass distribution along the soil profile. In each plot, three cores were taken within the crop rows in the middle of two adjacent maize plants. The soil cores were split into five segments of 12.5 cm length. Roots were carefully removed from the soil and cleaned before being dried at 60 °C for 3 days and weighed. The depth at which 50% of the root biomass occurred was then linearly interpolated. Crop yield was determined as dry silage yield 126 DAS on 28 September. Three rows from the centre of each plot were harvested and dried at 60 °C for 5 days before weighing.

### 2.5. Statistics

All statistical analyses were performed in R version 3.2.1 (R Core Team, 2015). Linear regressions between soil penetration resistance and matric suction were based on block mean values of each experimental treatment. Plant growth was analysed with a linear mixed model that accounts for effects of repeated measurements using the nlme package (Pinheiro et al., 2013).

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \delta_l + p_k + \varepsilon_{ijkl} \quad (1)$$

where  $Y$  denotes plant height and leaf number, respectively, in the  $i^{\text{th}}$  compaction treatment, the  $j^{\text{th}}$  tillage treatment, the  $l^{\text{th}}$  measurement date and the  $k^{\text{th}}$  plot;  $\alpha$  is the compaction effect,  $\beta$  the tillage effect,  $\alpha\beta$  is the effect of the interaction between compaction and tillage,  $\delta$  is the effect of the measurement date,  $p$  is the effect of the plot, and  $\varepsilon$  is the residual error. The plot was set as a random effect, and all other effects were treated as fixed effects. Two-way analysis of variance (ANOVA) was used to test for effects of tillage, compaction and their interaction on soil bulk density, soil porosity, root architectural traits, plant vigour traits at flowering, and final silage yield. Least significant difference (LSD) tests at  $p < .05$  were used to compare treatments means.

## 3. Results

The lowest soil bulk density and highest soil porosity, respectively, at 10 cm depth was observed in the uncompacted tilled (NC-T) and compacted tilled (C-T) treatment, followed by the uncompacted and untilled soil (NC-NT). Bulk density and total porosity at 10 cm depth

**Table 2**

Effects of compaction (Comp), tillage (Till) and their interaction on soil bulk density ( $\rho$ ) and total porosity ( $\varepsilon$ , calculated using particle density) analysed with analysis of variance (ANOVA). \*\* and \* denote significant effects at  $p < .01$  and  $p < .05$ , respectively, n.s. denotes non-significant effects ( $n = 3$ ). Treatment mean of the three blocks for compacted (C) and non-compacted (NC) soil that remained untilled (NT) or received tillage (T). Different letters indicate significant difference between treatment means using least significant difference tests at  $p < .05$ .

Property	Depth [cm]	ANOVA			Treatment mean			
		Comp	Till	Comp: Till	C-NT	C-T	NC-NT	NC-T
$\rho$ [ $\text{g cm}^{-3}$ ]	10	n.s.	*	n.s.	1.46a	1.38b	1.41ab	1.36b
	30	n.s.	*	n.s.	1.56	1.52	1.57	1.50
$\varepsilon$ [ $\text{cm}^3 \text{cm}^{-3}$ ]	10	$p = .08$	**	n.s.	0.44a	0.47b	0.46ab	0.48b
	30	n.s.	*	n.s.	0.41	0.42	0.41	0.43

was the highest and lowest, respectively, in the compacted no-till treatment (C-NT). No significant differences in porosity and bulk density between the treatments were observed at 30 cm depth (Table 2). Soil volumetric water content at field capacity (100 hPa) and the permanent wilting point (15,000 hPa) was similar across the four treatments. Consequently, the amount of plant available water was as well similar in all treatments (Supplementary data Fig. S1 and Fig. S2).

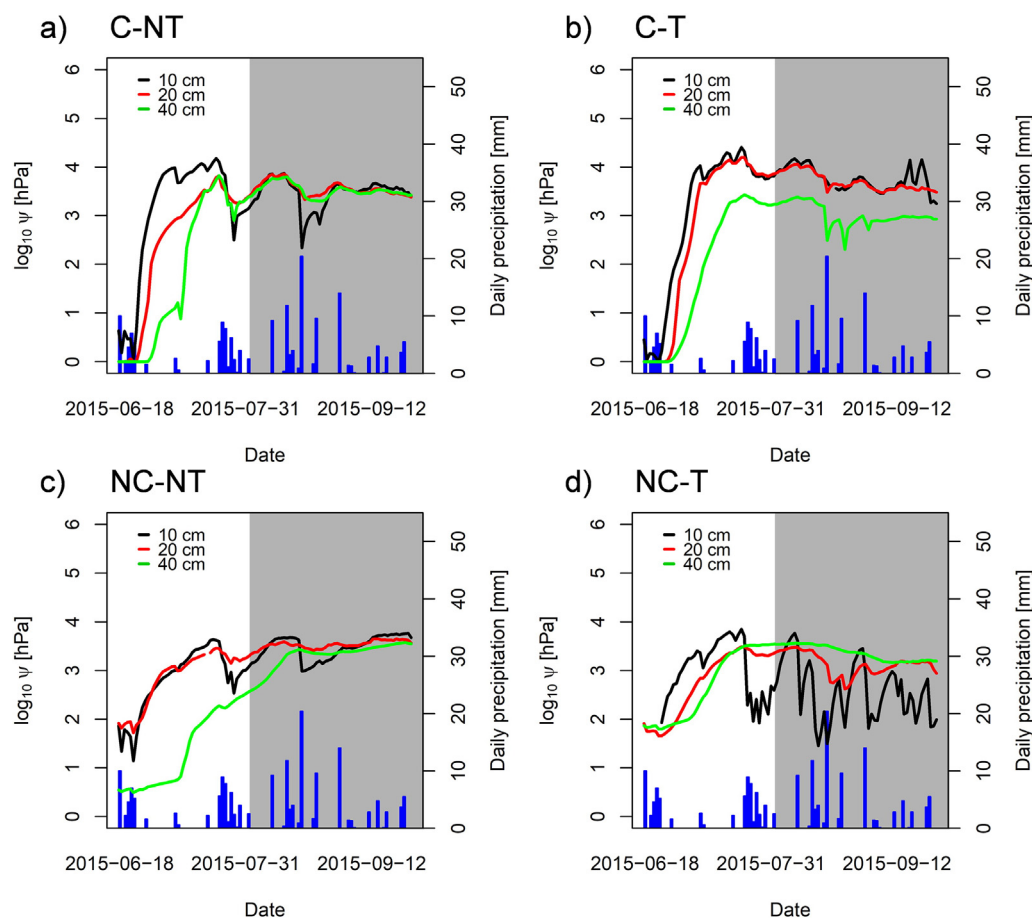
### 3.1. Soil moisture dynamics

Clear differences in soil moisture patterns were observed between the four soil treatments with respect to depth, indicating differences in water uptake by plants. Soil matric suction at 10 cm depth increased steadily after crop establishment and reached a first maximum in the middle of July around 50 DAS in all four treatments (Fig. 1). Except for NC-T, soil moisture remained more or less constant at this level until the end of the growing season in late September. Furthermore, soil rewetting at 10 cm after a rainfall did occur only weakly or not at all in C-T, NC-NT, C-NT. In contrast, soil matric suction at 10 cm in NC-T was fluctuating throughout the growing season, and these fluctuations coincided fairly well with precipitation events (Fig. 1). At 20 cm depth, soil moisture patterns over the growing season in C-T, NC-NT and NC-T were similar compared to those measured at 10 cm. In C-NT, soil drying depth occurred later at 20 cm than at 10 cm (Fig. 1).

The most pronounced effect of the different soil treatments on soil moisture dynamics was observed at 40 cm depth. Compared to NC-T, soil drying at 40 cm depth was delayed by several weeks in the other three treatments (Fig. 1). These differences in soil moisture dynamics implicate that the access to water pools by the crop varied between the treatments, particularly during vegetative plant development. The plants in NC-T were able to take up considerably more water from deeper soil layers during the time before flowering compared to the plants in NC-NT, C-T and C-NT. In particular in C-NT, water uptake was clearly restricted to the topsoil during vegetative crop development, which was reflected by the delayed soil drying at 20 and 40 cm (Fig. 1).

### 3.2. Soil penetration resistance

Penetration resistance in the topsoil varied between the different treatments and increased with increasing matric suction in all treatments (Fig. 2). At all evaluated soil water suctions, the highest penetration resistance was measured in C-NT. Penetration resistance in C-NT was  $>2$  MPa even under relatively moist conditions of 300 hPa, and exceeded 3 MPa at 1300 hPa matric suction (Fig. 2). The lowest soil penetration resistances at matric suctions of 300, 1000 and 2000 hPa was observed in NC-T. At 5000 hPa, measured penetration resistance was similar in NC-T, C-T and NC-NT. The threshold of 2 MPa penetration resistance was reached at a matric suction of approximately 2800 hPa in NC-T. In the C-T and NC-NT treatment, these thresholds were exceeded



**Fig. 1.** Soil moisture patterns during cropping season in 10, 20 and 40 cm depth in a) compacted and untilled soil (C-NT), b) compacted and tilled soil (C-T), c) uncompacted and untilled soil (NC-NT) and d) uncompacted and tilled soil (NC-T). Curves represent daily mean values of measurements from two sensor probes, and blue bars denote daily precipitation. Peak flowering occurred at 64 days after sowing and indicated the transition from vegetative (unshaded area) to generative (shaded area) plant development.

at lower water suctions, namely when matric suction reached 2200 hPa and 580 hPa, respectively. At around 5000 hPa matric suction, the penetration resistance threshold of 3 MPa was reached in NC-T, NC-NT and C-T (Fig. 2).

Linear regressions between soil matric suction and soil penetration resistance in combination with soil moisture recordings at 10 cm depth allowed identifying periods of the growing season during which penetration resistance exceeded 2 MPa and 3 MPa, respectively. In C-NT, soil penetration resistance of the topsoil was above 2 MPa during the entire growing season and often exceeded even 3 MPa. In contrast, soil penetration resistance at 10 cm depth in NC-T was only rarely above 2 MPa and never exceeded the threshold of 3 MPa. In the two other treatments – NC-NT and C-T – soil penetration resistance in the topsoil was below 2 MPa for the first five weeks of the growing season but then remained above 2 MPa during most of the following weeks until harvest. The threshold of 3 MPa was exceeded during several weeks in the C-T, whereas in the NC-NT soil penetration resistance was above 3 MPa just for 2 weeks at the end of the growing season (Fig. 2).

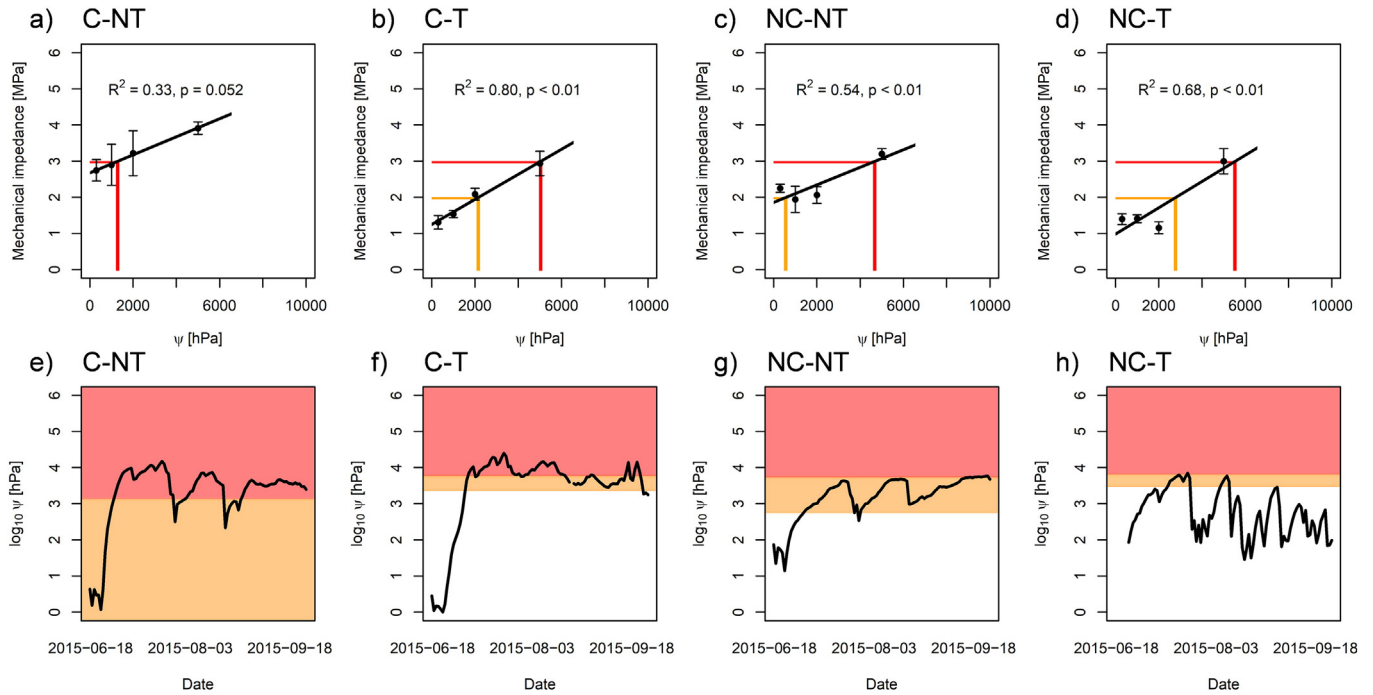
### 3.3. Maize phenotyping

Both soil compaction and the different tillage systems showed significant effects on the rate of plant growth during the vegetative development phase (Table 3). Plant height and leaf number, which were used as descriptors for plant growth, were the lowest in plants from C-NT followed by plants from NC-NT and C-T. Differences of plant height

between the treatments became evident towards the end of June, which corresponded to the 5-leaf stage and to around 30 DAS, respectively. Effects of the different treatments on leaf number occurred around three weeks later (Fig. 3). In spite of this difference in growth rate, peak flowering and thus the transition from vegetative to generative development was reached 64 DAS on 28 June in all treatments (Table 1). This was expected since maize phenology is bound to temperature sums, which was the same for all treatments.

At the time of root crown sampling 77 DAS on 10 August, plants in C-NT were 20% shorter and showed a 15% smaller stem diameter compared to plants in NC-T (Table 4). Plant height and stem diameter measured in plants from the other two treatments were smaller than in plants from NC-T but larger than in C-NT. Leaf greenness expressed in SPAD values was very similar for all treatments indicating no difference in leaf nitrogen content between the treatments (Table 4). The most pronounced effects of the different treatments on plant vigour were observed for final silage yield. Dry silage yield in C-NT and NC-NT were only 35% and 58%, respectively, of the yield obtained in NC-T. Silage yield in C-T was 89% of the yield in NC-T (Table 4).

As for plant vigour traits, significant differences between treatments were also observed for most of the assessed root system architecture traits. The number of nodal roots that penetrated soil was 25% lower in C-NT than in NC-T. Lateral branching density measured at 5 and 10 cm from the root base of nodal roots from the third whorl were reduced by 38% and 46%, respectively, in C-NT compared with NC-T (Table 4). The values for nodal root number and lateral branching density of nodal roots obtained for the other two treatments – C-T and NC-NT



**Fig. 2.** Linear regressions and multiple r-squared based on block mean values between soil matric suction and soil penetration resistance in soil samples taken at 10 cm depth from a) compacted and untilled soil (C-NT), b) compacted and tilled soil (C-T), c) uncompacted and untilled soil (NC-NT) and d) uncompacted and tilled soil (NC-T). Orange and red lines indicate soil matric suction above which penetration resistance exceeds 2 MPa and 3 MPa, respectively. Bars represent standard error ( $n = 3$ ). Soil moisture patterns during cropping season at 10 cm depth in e) compacted and untilled soil (C-NT), f) compacted and tilled soil (C-T), g) uncompacted and untilled soil (NC-NT) and h) uncompacted and tilled soil (NC-T). Orange and red shading indicate range of soil matric suction where penetration resistance is between 2 MPa and 3 MPa and  $>3$  MPa, respectively.

– were between the numbers reported for NC-T and C-NT. Similar differences were observed for the opening angle of the root crown, which was  $25^\circ$  wider in plants from NC-T compared to plants from C-NT. The number of whorls occupied with nodal roots did not vary significantly between treatments (Table 4). The width of the root crown obtained from image analysis with REST was 30% to 40% larger in C-NT compared to root crowns from the other treatments (Fig. 4). Significant treatment effects on the root phenotype were also obtained from image analysis on single roots. The median size of the background gaps within the single roots was significantly larger in NC-T compared to the other treatments suggesting a lower overall branching density of the root. Furthermore, the 1<sup>st</sup> quartile of the cluster diameter distribution, which served as a measure for global root diameter, was 20% larger in C-NT than in NC-T (Fig. 4).

The different treatments also influenced root dry biomass distribution along the soil profile. In both tilled treatments (NC-T and C-T) a steady increase of total root biomass was observed to a depth of 62.5 cm. In contrast, in the two no-till treatments (NC-NT and C-NT), dry root biomass was concentrated in the topsoil (Fig. 5). More than 50% of the dry root biomass was in the top 12.5 cm in both no-till treatments. In contrast, just 30% to 40% of the total root biomass were found in the top 12.5 cm of the tilled treatments. Therefore, the

interpolated depth at which 50% of the root biomass occurs was closer to the soil surface in the untilled plots compared to the tilled plots (Fig. 5).

#### 4. Discussion

In the current study, we quantified the interactions between soil penetration resistance, root system architecture and plant water uptake. This allowed us to show that feedbacks, which result from these interactions at the soil-root interface, determine water accessibility and therefore affect crop yields. As observed in previous studies, soil bulk density and porosity (Table 1) as well as soil penetration resistance (Fig. 2) were affected by soil compaction and differed between the two tillage systems (Barracough and Weir, 1988; Materechera et al., 1992; Botta et al., 2010; Hernandez-Ramirez et al., 2014; Colombi and Walter, 2016; Martínez et al., 2016). These soil structural and mechanical changes had significant impacts on root architecture, plant water extraction and plant growth and crop productivity.

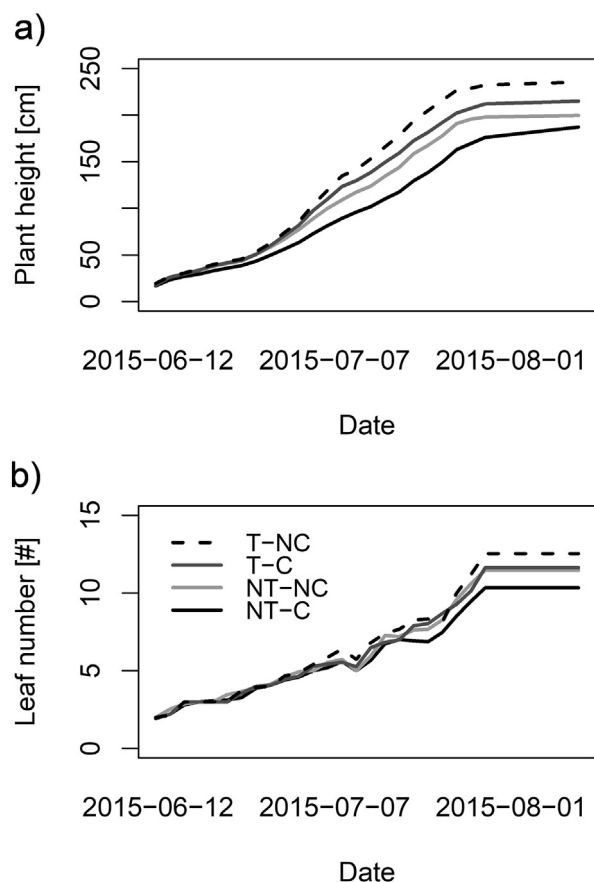
##### 4.1. Increased soil penetration resistance induced shallow root systems

Root system architecture differed among the assessed treatments. With increased topsoil penetration resistance, roots grew shallower, which was indicated by the root crown opening angle (Table 4) and the width of the root crown (Fig. 4). Root crowns were wider in the compacted no-till plots, which showed the highest penetration resistance, than in the uncompacted tilled plots, where the lowest penetration resistance was observed. This was consistent with findings for root biomass distribution along the soil profile. In the two tilled treatments,  $<40\%$  of the total root biomass was found in the uppermost 12.5 cm. In contrast, between 57% and 71% of the total root biomass was found in the top 12.5 cm in the two no-till treatments (Fig. 5). Furthermore, the number of lateral and axial roots were reduced and roots

**Table 3**

Effects of compaction (Comp), tillage (Till), their interaction and the day after sowing (DAS) on plant height and leaf number analysed using linear mixed models (Eq. (1)). \*\*, \* and n.s. denote significant effects at  $p < .01$  and  $p < .05$ , respectively, n.s. denotes non-significant effects ( $n = 3$ ).

	Comp	Till	Comp:Till	DAS
Plant height	*	**	n.s.	**
Leaf number	*	*	n.s.	**



**Fig. 3.** Vegetative plant development expressed as a) plant height and b) leaf number from two leaf stage at 18 days after sowing (DAS) until root crown sampling at 77 DAS. Curves denote treatment mean values of plots with uncompacted and tilled soil (NC-T), compacted and tilled soil (C-T), uncompacted and untilled soil (NC-NT) and compacted and untilled soil (C-NT) ( $n = 3$ ).

became thicker in response to increased topsoil penetration resistance (Table 4, Fig. 4). These findings correspond to results from previous studies on root architectural responses to increased penetration resistance in major crop species including maize (Barraclough and Weir, 1988; Materechera et al., 1992; Tracy et al., 2012; Grzesiak et al., 2013; Chen et al., 2014; Nosalewicz and Lipiec, 2014; Pfeifer et al., 2014; Colombi and Walter, 2016, 2017). Increased root growth in the topsoil, decreased root numbers as well as increased root diameters are well known acclimation strategies of plants to elevated soil

penetration resistance (Barraclough and Weir, 1988; Materechera et al., 1992; Chen et al., 2014; Colombi and Walter, 2016). These acclimation strategies help plants to overcome certain growth limitations that are imposed by increased soil penetration resistance. Previous studies have shown that, despite increased soil penetration resistance or increased soil bulk density, plant growth and crop productivity are not always decreased (Czyż, 2004; Arvidsson and Håkansson, 2014; Hernandez-Ramirez et al., 2014). However, shallower root systems, decreased root numbers and thicker roots reduce the volume of soil that plants can exploit to acquire water and nutrients.

#### 4.2. Feedbacks between soil penetration resistance, root architecture and water uptake restricted water accessibility

The alterations in root architecture due to increased soil penetration resistance affected water extraction by plants, and thus soil moisture dynamics throughout the cropping season. This was particularly pronounced when comparing the compacted no-till treatment with the uncompacted and tilled treatment. In the uncompacted and tilled soil, plants had access to water from deeper soil layers relatively early during vegetative growth, which is indicated by soil moisture patterns at 40 cm depth obtained from in-situ soil moisture recordings. In comparison, water extraction and thus soil drying at 20 cm and 40 cm in the compacted no-till treatment was delayed (Fig. 1). Furthermore, rewetting of the soil at 10 cm depth after a rainfall event was clearly observable in the uncompacted and tilled soil but not in the compacted no-till treatment (Fig. 1). The seasonal soil moisture pattern in the two other treatments – compacted tilled and uncompacted no-till – were similar to the pattern observed in the compacted and untilled soil (Fig. 1). Hence, increased topsoil penetration resistance led to increased water uptake from the topsoil and at the same time decreased water uptake from deeper layers, which is in line with results from pot and field studies (Araki and Iijima, 2005; Nosalewicz and Lipiec, 2014; Siczek et al., 2015).

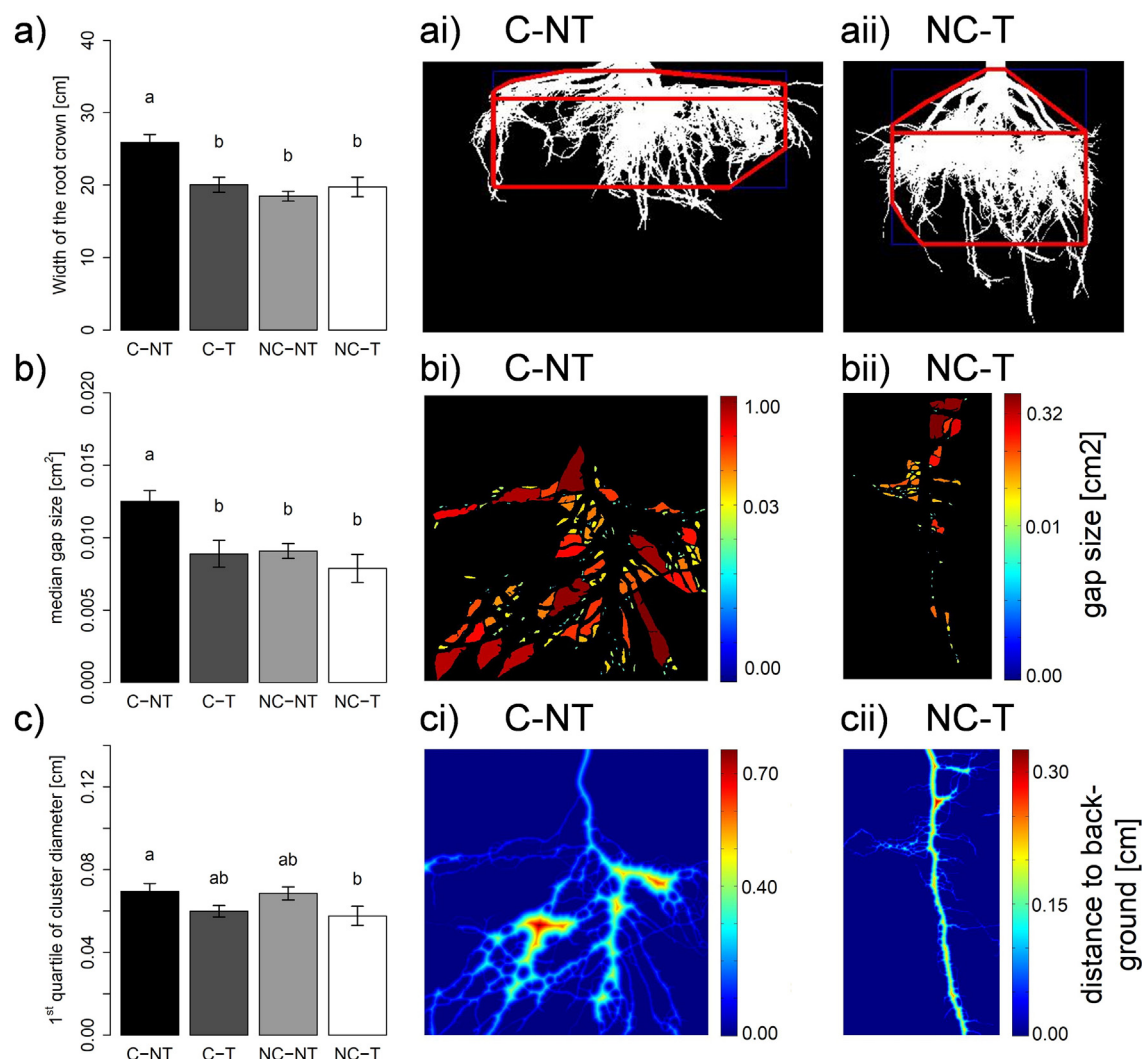
Topsoil penetration resistance is critical for maize since its root system is dominated by shoot-borne nodal roots, which are initiated close to the soil surface (Kutschera and Lichtenegger, 1960; Abendroth et al., 2011). Soil penetration resistance at 10 cm depth increased with increasing matric suction in all four treatments (Fig. 2). This observed linear relationship between soil moisture and penetration resistance ultimately implies that soil penetration resistance was not constant during the growing season. Even though this interaction is known, it is rarely taken into account in studies investigating plant growth in compacted as well as dry soils (Bengough et al., 2011). We used the relationship between soil penetration resistance and soil moisture to determine matric suctions above which penetration resistance exceeded 2 MPa and 3 MPa, respectively. In combination with in-situ soil moisture monitoring,

**Table 4**  
Effects of compaction (Comp), tillage (Till) and their interaction on root system architecture and plant vigour traits after flowering and dry silage yield analysed with analysis of variance (ANOVA). \*\* and \* denote significant effects at  $p < .01$  and  $p < .05$ , respectively, n.s. denotes non-significant effects ( $n = 3$ ). Treatment mean of the three blocks for compacted (C) and non-compacted (NC) soil that remained untilled (NT) or received tillage (T). Different letters indicate significant difference between treatment means using least significant difference tests at  $p < .05$ .

Trait	ANOVA			Treatment mean			
	Comp	Till	Comp:Till	C-NT	C-T	NC-NT	NC-T
NoWh [#]	n.s.	n.s.	n.s.	5.0	4.9	4.9	5.1
NoNR [#]	*	*	n.s.	29.5a	33.2a	33.6a	39.1b
NoLR [# cm <sup>-1</sup> ]							
5 cm from root base	n.s.	$p = .09$	n.s.	11.4b	15.4ab	14.6ab	21.0b
10 cm from root base	*	*	n.s.	11.1a	12.5a	13.3a	17.9b
Root crown opening angle [°]	**	**	$p = .09$	162a	146b	143bc	137c
SPAD	n.s.	n.s.	n.s.	55.2	54.5	54.0	53.1
Plant height [cm]	n.s.	**	n.s.	188a	214ab	198a	234b
Stem diameter [mm]	**	n.s.	n.s.	19.8a	20.9ab	22.3bc	23.3c
Dry silage yield [Mg ha <sup>-1</sup> ]	**	**	n.s.	5.9a	15.2c	9.9b	17.1c

Abbreviations: NoWh = number of whorls occupied with nodal roots, NoNR = number of nodal roots, NoLR = number of lateral roots in nodal roots from the third whorl.





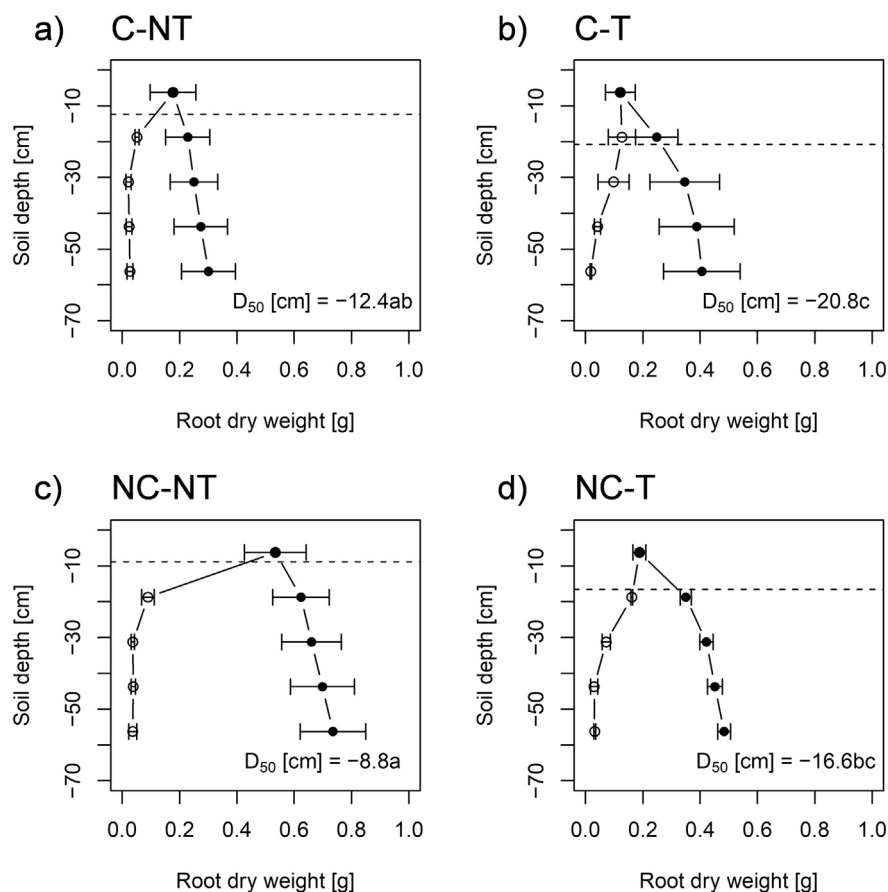
**Fig. 4.** Results from image processing with REST: a) width of the root crown, b) median size of gaps within a single root and c) 1<sup>st</sup> quartile of cluster diameters of a single root obtained from the distance map. Bars represent treatment means for plants from compacted and untilled soil (C-NT), compacted and tilled soil (C-T), uncompacted and untilled soil (NC-NT) and uncompacted and tilled soil (NC-T). Different letters indicate significant difference between the treatment means using least significant difference tests at  $p < .05$ , bars represent standard error ( $n = 3$ ). Typical pictures of plants from i) C-NT and ii) NC-T analysed for the respective traits.

this enabled us to show that penetration resistance at 10 cm depth of the uncompacted and tilled soil was rarely above 2 MPa and never exceeded 3 MPa. Penetration resistance in the uncompacted no-till and the compacted tilled soil varied between  $<2$  MPa and  $>3$  MPa. In contrast, topsoil penetration resistance in the compacted no-till treatment, was above 2 MPa during the entire cropping season and even above 3 MPa for a large part of the growing season (Fig. 2). Other studies showed that above these thresholds, soil penetration resistance becomes the major factor limiting root elongation (Bengough et al., 2011; Valentine et al., 2012). The differences in topsoil penetration resistance resulted partially from the effects of the different tillage and compaction treatments on soil bulk density (Table 2). However, the alterations of root architecture caused by increased penetration resistance, namely shallower root growth (Fig. 4 and Table 4), enforced water extraction from the topsoil (Fig. 1). In return, this led to even higher topsoil penetration resistance (Fig. 2), impeded root growth into deeper layers (Fig. 5) and ultimately reduced the access of roots to abundant water in the subsoil (Fig. 1). To the best of our knowledge, this feedback between soil penetration resistance, root architecture and plant water uptake has not been shown previously.

#### 4.3. Limited water accessibility decreased crop growth and productivity

Decreasing plant growth rates due to increased soil penetration resistance has been shown for different crop species both in the field and under controlled conditions (Young et al., 1997; Colombi and Walter, 2017; Colombi et al., 2017a). In the current study, increased topsoil penetration resistance coincided with decreased plant growth rates (Fig. 3). Besides significant effects of the treatments on plant growth (Table 3), high topsoil penetration resistance also reduced plant vigour at flowering (Table 4). As green biomass in maize is accumulated before flowering (Abendroth et al., 2011), vegetative growth largely determines the photosynthetic capacity during generative development. Therefore, vegetative development is critical for both silage and grain yield. We showed here that reduced plant growth rate before flowering due to increased soil penetration resistance (Fig. 3) coincided with reduced silage yield (Table 4). Decreased crop vigour and productivity in response to increased soil penetration resistance at the field scale were reported in previous studies (Barracough and Weir, 1988; Botta et al., 2010; Colombi and Walter, 2016; Colombi et al., 2017a). The literature on effects of soil penetration resistance on phosphorus uptake by





**Fig. 5.** Root dry matter (open symbols) and cumulative root dry matter distribution (closed symbols) along the soil profile in a) compacted and untilled soil (C-NT), b) compacted and tilled soil (C-T), c) uncompacted and untilled soil (NC-NT) and d) uncompacted and tilled soil (NC-T). Dashed line represents depth at which 50% of the roots occurred ( $D_{50}$ ). Different letters indicate significant difference between the treatment means using least significant difference tests at  $p < .05$  and bars represent standard errors ( $n = 3$ ).

crops is not unanimous: both increased and decreased phosphorus acquisition was observed (Kristoffersen and Riley, 2005; George et al., 2011; Pfeifer et al., 2014). Leaf greenness represented by SPAD values, which are good predictors for nitrogen nutrition of plants (Weih et al., 2011), was not affected by increased soil penetration resistance (Table 4). The results from the current study, namely the observed soil moisture dynamics (Fig. 1) and root architectural properties (Table 4, Fig. 4, and Fig. 5), strongly suggest that the treatment differences in crop growth and productivity were mainly caused by differences in water uptake. Hence, crop growth and yield depended on the potential of plant roots to access water in the subsoil, which in turn was determined by topsoil penetration resistance.

## 5. Conclusion

With the current study, we demonstrated that interactive effects between soil penetration resistance, root architecture and plant water uptake determine water accessibility by roots and ultimately affect crop growth. Root growth became shallower in response to increased topsoil penetration resistance, which increased water uptake from the topsoil. In return, this led to further increased topsoil penetration resistance. As a consequence of this feedback, root growth into deeper soil layers and thus water uptake from the subsoil was restricted, which decreased plant growth and crop productivity. Hence, we showed that water limited crop yields may result from limited water accessibility, which is largely caused by high penetration resistance. This has implications for the development of strategies aiming to mitigate water limitations on crop yields, which includes drought tolerant crop varieties and optimised irrigation schemes. Water accessibility and thus the potential of roots to reach abundant and available soil water pools needs to be

considered in order to ensure crop productivity under drier conditions. To be successful, such initiatives should therefore account for the interactions of root growth, soil penetration resistance and plant water uptake and their feedbacks on water accessibility and crop yields.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2018.01.129>.

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